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# ON THE RELATIVE DIMENSIONS OF THE OSSEOUS SEMICIRCULAR CANALS OF BIRDS.<sup>1</sup>

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The purpose of this paper has been to determine whether there is any relation of the comparative dimensions of the bony semicircular canals of the ear of birds, either to mode of locomotion, or to genetic affinities.

These precise questions have apparently not been considered, except in a short paper by Farrar (1831) that was inaccessible to me. Indeed there has been no extended comparative study of the dimensions of these bony canals, though the inner ear labyrinth has been carefully investigated, notably by Retzius (1884).

In all cases my dissections were made on dried adult skulls. The material used was the collection of the University of Texas. All the American specimens studied had been identified by Prof. Montgomery, and exotic ones by the dealers from whom they were secured.

The work was done entirely under the direction of Prof. Montgomery, to whom I am greatly indebted for his valuable assistance and encouraging sympathy.

## I. MODES OF LOCOMOTION IN BIRDS.

*Archæopteryx*, the earliest known bird, was a good flyer if we may judge from its possession of a sternal keel, but it also used its fore-limbs as grasping organs since they were provided with free unguiculate digits.

What has given birds their superiority over the reptiles was the acquisition of flight, and the main avian peculiarities are referable to this mode of locomotion. Birds may have developed flight in one of two ways — by saltatory locomotion, whereby the hind limbs were used as propellers, and the fore-limbs as organs of balance ; or by scansorial locomotion on trees, whereby

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the fore-limbs came to be used as parachutes in the aerial passage from one tree to another. The second of these ways may have been the more probable. No modern birds use their wings in the manner of legs, except the young of *Opisthocomus*, but employ them rather as organs of flight, as balancers or as flippers (penguins).

The different modes of locomotion are intimately connected. In this study of the bearing of the relation of the size of the semi-circular canals to the mode of locomotion, the following main kinds of locomotion were distinguished: The *cursorial*, where the hind limbs are employed to the greatest extent, and upon the hard ground; of such birds I have examined the ostrich and roadrunner. The *arboreal*, where wings and feet are employed about equally, as in most of the passerines. A modification of the preceding is the *scansorial* locomotion of such birds as woodpeckers. The *volant*, where the wings are used to the greatest extent, as in all birds of long sustained flight; those with the power of soaring represent the acme of this mode of locomotion. The combination of *volant* and *nektant*, that is of strong flight with the power of swimming, as in the gulls and albatrosses. The *pygopodal*, which may be swimming under water (grebes), or flight under the water (penguins). The *grallatorial*, where the birds walk upon moist or yielding ground, with an elongation or partial webbing of the toes; such birds have either a strong or weak power of flight and some of them can swim to a slight extent.

In the evolution of these modes of locomotion a climbing, arboreal habit was probably earliest. From this would have followed divergently: (*a*) development of stronger flight, and more aerial life; (*b*) loss of flight and terrestrial running; (*c*) development of a wading habit. Swimming birds have probably descended from waders and divers from swimmers. The most modified birds, from the standpoint of locomotion, would be the two very different groups of flightless birds, the Ratitæ and the Sphenisci.

In any study of genetic relationships of birds one may find some help in considering the evolution of modes of locomotion.

## 2. DIMENSIONS OF THE CANALS.

The right ear was the one studied in all cases, and the semicircular canals laid bare by the knife. To measure these curved canals a piece of No. 50 cotton thread was drawn around each and the length marked on it; then the exact length of the thread when straightened out was ascertained. All absolute dimensions are stated in millimeters. All measurements were made twice, at an interval of time, in order to secure the greatest possible accuracy. For units of comparison a median vertical and a median basilar cranial length were employed. The vertical length is the distance from the ventral face of the occipital condyle to the large transverse muscle crest immediately above the foramen magnum; the basilar length is the distance from the posterior face of the condyle to the anterior aperture of the Eustachian tube as marked by bony ridges. These were taken as units of comparison because they can be very accurately measured, but especially because they are lengths of parts of the skull that are perhaps the least subject to variation.

In the tables the first three vertical columns give the absolute lengths of the semicircular canals. The fourth and fifth columns give the absolute basilar and vertical lengths of the skull for comparison. The succeeding three columns show which of the canals are largest. The ninth column gives as the "combined measurement" of comparison the sum of the vertical and basilar cranial lengths divided by two. The tenth column expresses the sum of the absolute lengths of all three canals. And the last column represents this sum divided by the combined cranial measurement given in the ninth column. This last column, accordingly, states the sum of the lengths of the three canals in relation to a definite length of the skull, and may be called the "relative total length."

A comparison of the figures given in the last column of the tables shows what genera have the relatively larger, and what ones the relatively smaller canals, expressed in terms of the cranial measurements. We find then the following associations according to this relative sum total length of the canals:

1.00 mm. to 1.25 mm., the one genus *Pelecanus*.

1.25 mm. to 1.49 mm., *Struthio*, and certain Anatidæ (*Anas*).

Family and Genus.	Length of Anterior.	Length of Posterior.	Length of Extremity.	Basal Measurement.	Vertical Measurement.	Posterior Largest.	Extremity Largest.	Extremity and Posterior Equal.	Combined Measurement.	Sum of Three Canals.	Relative Total Length.
Struthionidae.											
<i>Struthio camelus</i> Linn.....	32	18	14	43	43	×			43	64	1.49
Spheniscidae.											
<i>Eudytes minor</i> .....	18	13	11	23	26	×			24	42	1.75
Phalacrocoracidae.											
<i>Phalacrocorax mexicanus</i> (Brandt.) .....	12	9	10	16	18		×		17	31	1.82
Pelecanidae.											
<i>Pelecanus erythrorhynchus</i> Gmel.....	17	11	11	31	35			×	33	39	1.18
Ardeidae.											
<i>Ardea herodias</i> Linn.....	19	12	13	18	19		×		18	44	2.44
" <i>rufescens</i> Gmel.....	12	10	10	15	14			×	14	32	2.28
" " ".....	15	9	10	15	15		×		15	35	2.33
" " ".....	12	8	9	12	11.9		×		12	29	2.41
<i>Nycticorax nycticorax naevius</i> (Bodd.) .....	15	12	13	16	16		×		16	40	2.49
Ciconiidae.											
<i>Ciconia</i> (? <i>C. alba</i> .) .....	21	13	12	28	27	×			27	46	1.70
Anatidae.											
<i>Defila acuta</i> (Linn.) .....	11	9	10	19	18		×		18	30	1.66
<i>Aythya americana</i> (Eyt.) .....	12	9	10	20	20		×		20	31	1.55
<i>Anas boschas</i> Linn.....	12	10	9	23	23	×			23	31	1.43
<i>Chen hyperborea</i> (Pall.) .....	15	8	10	21	20		×		20	33	1.65
<i>Nettion carolinensis</i> (Gmel.) .....	9	6	7	15	14		×		14	22	1.57
<i>Anser albifrons gambeli</i> (Hartl.) .....	13	10	10	20	21			×	20	33	1.65
" " ".....	13	10	10	20	21			×	20	33	1.65
<i>Querquedula discors</i> (Linn.) .....	10	7	8	14	14		×		14	25	1.78
Cathartidae.											
<i>Catharista urubu</i> (Vieill.) .....	20	11	12	20	23		×		21	43	2.04
<i>Cathartes aura</i> (Linn.) .....	17	12	12	18	18			×	18	41	2.27
Falconidae.											
<i>Buteo borealis</i> (Gmel.) .....	21	17	15	18	20	×			19	53	2.78
<i>Falco columbarius</i> Linn.....	15	12	12	10	15			×	12	39	3.25

Family and Genus.	Length of Anterior.	Length of Posterior.	Length of Exterior.	Basal Measurement.	Vertical Measurement.	Posterior Largest.	Exterior Largest.	Exterior and Posterior Equal.	Combined Measurement.	Sum of Three Canals.	Relative Total Length.
Tinamidae.											
<i>Tinamus brasiliensis</i> .....	15	11	10	16	12	×			14	36	2.57
Tetraonidae.											
<i>Colinus virginianus</i> (Linn.).....	10	8	9	12	10		×		11	27	2.45
“ “ .....	10	7	8	10	8		×		9	25	2.77
<i>Callipepla squamata</i> (Vig.) .....	10	7	8	9	9		×		9	25	2.77
“ “ .....	10	7	8	10	9		×		9	25	2.77
“ “ .....	10	7	8	10	9		×		9	25	2.77
<i>Cyrtonyx montezumae mearnsi</i> (Nels.) .....	11	9	9	12	9			×	10	29	2.90
Phasianidae.											
<i>Meleagris gallopavo</i> Linn. ....	17	13	11	22	21	×			21	41	1.99
<i>Gallus bankiva</i> Linn. ....	14	12	10	18	10	×			17	36	2.11
Rallidae.											
<i>Falica americana</i> Gmel. ....	14	9	10	14	13				13	33	2.53
<i>Rallus</i> .....	13	9	10	14	13		×		13	32	2.46
<i>Porzana</i> .....	11	6	7	9	8		×		8	24	3.00
Gruidae.											
<i>Grus mexicana</i> (Müll.) .....	18	11	12	19	20		×		19	41	2.15
Charadriidae.											
<i>Squatarola squatarola</i> (Linn.) .....	16	10	11	11	12				11	37	3.36
“ “ .....	13	10	11	11	12				11	34	3.09
<i>Charadrius</i> .....	12	9	9	9	10			×	9	30	3.33
<i>Aegialitis wilsonia</i> (Ord) .....	8	7	6	8	9	×			8	21	2.62
<i>Aegialitis vocifera</i> (Linn.) .....	9	7	7	10	9			×	9	23	2.77
Scolopacidae.											
<i>Numenius longirostris</i> Wils. ....	13	8	8	9	10			×	9	29	3.22
<i>Gallinago delicata</i> (Ord.) .....	13	8	8	9	10			×	9	29	3.22
<i>Tringa maculata</i> (Vieill.) .....	9	6	7	8	8		×		8	22	2.75
<i>Tringa bairdii</i> (Coues) .....	9	5	6	9	8				8	20	2.50
<i>Ereunetes pusillus</i> (Linn.) .....	8	5	6	7	6				6	19	3.16
“ “ .....	8	5	6	7	6				6	19	3.16

Family and Genus.	Length of Anterior.	Length of Posterior.	Length of Exterior.	Basal Measurement.	Vertical Measurement.	Posterior Largest.	Exterior Largest.	Exterior and Posterior Equal.	Combined Measurement.	Sum of Three Canals.	Relative Total Length.
<b>Scolopacidae.—Continued.</b>											
<i>Calidris arenaria</i> (Linn.) .....	8	6	6	7	7			×	7	20	2.85
<i>Totanus melanoleucus</i> (Gmel.) .....	12	8	9	11	10		×		10	29	2.90
<i>Totanus flavipes</i> (Gmel.) .....	11	7	8	9	8		×		8	26	3.25
<i>Symphemia semipalmata inornata</i> (Brewst.) .....	13	9	9	12	11			×	11	31	2.81
<b>Aphrizaide.</b>											
<i>Arenaria morinella</i> (Linn.) .....	11	8	7	9	10	×			9	26	2.88
<b>Laridae.</b>											
<i>Larus atricilla</i> Linn. ....	16	8	7.5	13	12.3	×			13	31	2.38
<i>Larus delawarensis</i> Ord. ....	15	9	8	14	12	×			13	32	2.46
<i>Sterna maxima</i> Bodd. ....	14	10	8	15	17	×			16	32	2.00
<b>Stercorariidae.</b>											
<i>Stercorarius longicaudus</i> (Viell.) .....	14	10	9	13	14	×			13	33	2.53
<b>Columbidae.</b>											
<i>Columba fasciata</i> (Say) .....	14	9	10	12	13		×		12	33	2.91
<i>Columba oenas</i> .....	14	9	8	12	11		×		11	31	2.81
<i>Turtur auritus</i> .....	12	7	6	10	9		×		9	25	2.77
<i>Zenaidura macroura</i> (Linn.) .....	10	6	7	9	9				9	23	2.66
<b>Cuculidae.</b>											
<i>Geococcyx californianus</i> (Less.) .....	18	8	11.5	14	13		×		13	31	2.84
<b>Psittacidae.</b>											
<i>Psittacus erythacus</i> .....	13	10	10	17	15			×	16	33	2.06
<b>Alcedinidae.</b>											
<i>Ceryle alcyon</i> (Linn.) .....	13	10	9	12	13	×			12	32	2.66
<b>Strigidae.</b>											
<i>Syrinx nyctea</i> Linn. ....	23	18	15	18	17	×			17	56	3.29
<b>Bubonidae.</b>											
? <i>Asio accipitrinus</i> (Pall.) .....	15	12	11	15	14	×			14	38	2.71
<b>Caprimulgidae.</b>											
<i>Phalaenoptilus nuttallii nitidus</i> (Brewst.) .....	11	6	7	9	8		×		8	24	3.00
<i>Chordeiles virginianus</i> (Gmel.) .....	11	8	8	9	10				9	27	3.00

Family and Genus.	Length of Anterior.	Length of Posterior.	Length of Exterior.	Basal Measurement.	Vertical Measurement.	Posterior Largest.	Exterior Largest.	Exterior and Posterior Equal.	Combined Measurement.	Sum of Three Canals.	Relative Total Length.
Caprimulgidae.—Continued.											
<i>Chordeiles acutipennis texensis</i> (Lawr.).....	11	8	8	8	9			×	8	27	3.37
Trochilidae.											
<i>Trochilus colubris</i> (Linn.).....	5	4	4	3.8	3			×	3	13	4.33
Picidae.											
<i>Dryobates villosus harrisi</i> (Aud.).....	10	8	9	10	11		×		10	27	2.70
<i>Dryobates pubescens</i> (Linn.).....	9	7	7	9	8			×	8	23	2.87
<i>Dryobates scalaris boirdi</i> (Malh.).....	10	8	8	9	10			×	9	26	2.88
<i>Melanerpes erythrocephalus</i> (Linn.).....	12	9	10	9	10			×	9	31	3.44
<i>Colaptes auratus luteus</i> Bangs.....	13	10	12	13	12			×	12	35	2.91
Tyrannidae.											
<i>Myiarchus cinerascens</i> (Lawr.).....	9	6	7	9	9		×		9	22	2.44
Corvidae.											
<i>Corvus americanus</i> Aud.....	16	11	13	14	15		×		14	40	2.92
Icteridae.											
<i>Molothrus ater</i> Bodd.....	9	6	7	7	7				7	22	3.14
<i>Sturnella magna hoopesi</i> Stone.....	10	6	8	10	10				10	24	2.00
Fringillidae											
<i>Amphispiza bilineata deserticola</i> (Ridgw.).....	7	5	6	6	6		×		6	18	3.00
Tanagridae.											
<i>Piranga rubra</i> (Linn.).....	9	7	7	8	8			×	8	23	2.87
Hirundinidae.											
<i>Fregata subis</i> (Linn.)... ..	9	6	5	9	9	×			9	20	2.22
Mniotiltidae.											
<i>Dendroica coronata</i> (Linn.).....	8	4	5	6	6		×		6	17	2.83
Troglodytidae.											
<i>Galeoscoptes carolinensis</i> (Linn.).....	9	6	7	9	9		×		9	22	2.44
Paridae.											
<i>Parus atricristatus</i> (Cass.) .....	8	6	6	8	8			×	8	20	2.50
Turdidae.											
<i>Merula migratoria</i> (Linn.) .....	10	7	8	9	9		×		9	25	2.77

1.50 mm. to 1.74 mm., the families Ciconiidae, Anatidae (*Dafila*, *Aythya*, *Chen*, *Nettion*, *Anser*).

1.75 mm. to 1.99 mm., the families Spheniscidae, Phalacrocoracidae, and Anatidae (*Querquedula*).

2.00 mm. to 2.22 mm., the families Carthartidae (*Cartharista*), Gruidae, Phasianidae, Laridae (*Sterna*), Psittacidae.

2.23 mm. to 2.46 mm., the families Ardeidae (*Ardea*), Cathartidae (*Carthartes*), Tetraonidae (*Colinus*), Laridae (*Larus*), Tyrannidae, Hirundinidae and Troglodytidae.

2.47 mm. to 2.70 mm., the families Ardeidae (*Nycticorax*), Tinamidae, Rallidae (*Fulica*, *Rallus*), Charadriidae (*Ægialites*), Scolapacidae (*Tringa*), Stercorariidae, Columbidae (*Zenaidura*), Alcedinidae and Paridae.

2.71 mm. to 2.94 mm., the families Falconidae (*Buteo*), Picidae (*Dryobates*, *Colaptes*), Tetraonidae (*Colinus*, *Callipepla*, *Cyrtonyx*), Charadriidae (*Ægialites*), Turdidae, Scolapacidae (*Tringa*, *Calidris*, *Totanus*, *Symphemia*), Aphrizidae, Columbidae (*Columba*, *Turtur*), Mniotiltidae, Cuculidae and Tanagridae.

2.95 mm. to 3.18 mm., the families Rallidae (*Porzana*), Charadriidae (*Squatarola*), Scolapacidae (*Ereunetes*), Icteridae, Caprimulgidae (*Phalænoptilus*, *Chordeiles*), and Fringillidae.

3.18 mm. to 3.32 mm., the families Falconidae (*Falco*), Strigidae and Scolapacidae (*Numenius*, *Gallinago*).

3.32 mm. to 3.56 mm., the families Charadriidae (*Squatarola*, *Charadrius*), Caprimulgidae (*Chordeiles*) and Picidae (*Melanerpes*).

4.33 mm., the family Trochilidae.

These data show that birds of the most diverse forms of locomotion, and of very diverse affinities may show the same relative sizes of semicircular canals. For example an excellent flyer, the black vulture (*Catharista*), and the poor flyers, the chicken (*Gallus*) and the parrots (Psittacidae), have the same relative measurement, 1.98 mm. to 2.22 mm. Further, in certain families the genera may exhibit great differences in these measurements, as particularly in the Charadriidae and Anatidae.

The relative sizes of the three semicircular canals to each other may be summed up as follows :

The anterior canal is always the largest.

The posterior canal is larger than the exterior in all the follow-

ing families: Struthionidæ, Spheniscidæ, Ciconiidae, Tinamidæ, Phasianidæ, Aphrizidæ, Laridæ, Strigidæ, Stercorariidæ, Alcedinidæ, Bubonidæ, and Hirundinidæ.

The exterior canal is larger than the posterior canal in the families: Phalacrocoracidæ, Cuculidæ, Tyrannidæ, Corvidæ, Icteridæ, Fringillidæ, Mniotiltidæ, Troglodytidæ, and Turdidæ.

The posterior and exterior canals are equal in the families: Pelecanidæ, Tanagridæ, and Paridæ.

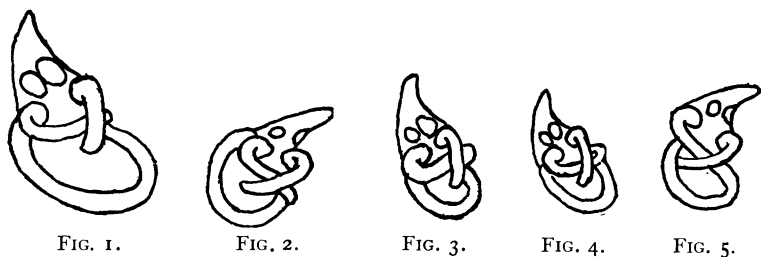
The posterior canal is larger than the exterior, or the posterior and exterior canals are equal, in the family Falconidæ.

The exterior canal is larger than the posterior canal, or the exterior and posterior canals are equal, in the families; Ardeidæ, Cathartidæ, Tetraonidæ, Caprimulgidæ, and Picidæ.

Falling under none of the above groups are the families: Anatidæ, Charadriidæ, Scolapacidæ, and Columbidae; in each of which there are great generic differences of the relative sizes of the canals.

### 3. TYPES OF CANALS.

In taking the measurements of the canals, I noticed that the position of the canals with reference to one another or the angle at which they are joined, was not always the same. There are



five types, though these intergrade, under which all species may be grouped (Figs. 1-5). It will be noticed that these are differences mainly of the anterior canal, depending on its length.

Type I. (Fig. 1), the genera *Struthio* and *Tinamus*.

Type II. (Fig. 2), Cathartidæ, *Geococcyx*, Scolopacidæ, Laridæ, *Stercorarius*, *Columba*, *Zenaidura*, *Ceryle*, Caprimulgidæ, *Strix*, *Asio*, Tetraonidæ.

Intermediate between types III. and V. are the genera *Turtur*, *Melanerpes*, and *Dryobates*.

Type III. (Fig. 3), *Ardea*, *Phalacrocorax*, *Ara*, Anatidæ.

Type IV. (Fig. 4), *Ciconia*, Rallidæ, *Grus*, *Eudytes*, *Psittacus*.

Intermediate between III. and IV. are the genera *Pelecanus*, and *Meleagris*.

Type V. (Fig. 5), *Falco*, Charadriidæ, *Colaptes*, *Trochilus*, and the Passeres.

In the above, as in the results from the comparison of the measurements, the types of canals bear no relation to locomotion; for different genera having very different modes of locomotion have the same type of canal; for example in type II. occurs *Catharista*, one of the best flyers, and in the same group *Geococcyx* which seldom flies but is one of the ablest runners.

#### 4. EUSTACHIAN TUBE APERTURES.

The Eustachian tubes have a common œsophageal opening in all cases, except in the genera *Struthio*, *Eudytes* and *Tinamus*, where there is a pair of apertures.

The Eustachian tube is a perfect bony tube in the following: *Sterna*, *Squatarola*, *Ceryle*, *Psittacus*, *Geococcyx*, Tetraonidæ, Phasianidæ, *Catharista*, *Falco*, *Eudytes*, and *Tinamus*. In all other cases it is imperfectly ossified.

#### CONCLUSIONS.

From a careful consideration of all the preceding data, the following conclusions may be drawn:

1. The anterior canal is always the largest.
2. The exterior canal is larger than the posterior in the greater number of cases.
3. The relative measurements of the canals to each other, as well as their sums, bear no direct relation to modes of locomotion.
4. Relative dimensions certainly stand in no relation to broader racial affinities and such dimensions can be used as taxonomic characters only to limited extent.
5. What occasions differences in these dimensions remains to be determined.
6. The anterior vertical canal is the one most subject to variation of position.

7. Types of bony labyrinths, distinguished according to relative positions of the canals, appear to stand in no relation to mode of locomotion, but to 'a certain extent are indicative of genetic affinity.

8. There are two main modes in the position of the pharyngeal aperture of the Eustachian tubes: a common pharyngeal aperture, or two distinct ones.

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